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# PURE LINE INHERITANCE AND PARTHENOGENESIS.

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## INTRODUCTION.

Ever since Johanssen, by his epoch-making researches with self-fertilized strains of beans, established his pure line conception of heredity, other investigators have been extending this conception so as to have it include many forms which do not reproduce sexually. In fact some of these investigators hold that all selections made within isolated strains of asexually reproducing plants and animals will fail to alter in the least the fraternal mean of succeeding generations.

Some careful work already has been done with lower organisms, which shows that Johanssen's pure line conception holds true for forms reproducing by fission or budding. Up to the present time no extensive work has been done with parthenogenetic animals. In fact the only paper which I have found dealing with selections among parthenogenetic forms is one by Kelly. Kelly worked with an aphid, *Aphis rumicis*, but did not carry his selections beyond two generations. However, he came to the conclusion that, "the progeny does not inherit the somatic idiosyncrasies of the parent, but does inherit from the underlying germ plasm common to all."

During the winter of 1910-'11, I began a series of experiments along pure lines with the cabbage aphid, *Aphis brassicæ* Linn., but while moving about from one part of the country to another I confined the individuals too closely in their breeding cells with the unfortunate result that they all died.

Again during the summer of 1912 I took up similar experiments with our common black cherry aphid, *Myzus cerasi* Fab., but before I obtained a sufficient number of generations to make the results reliable, cold weather set in causing the sexual forms to appear, thus spoiling my results.

While working this last winter with the European grain aphid, *Aphis avenæ* Fab., I noticed its great variations, and since the

species was already reproducing parthenogenetically under laboratory conditions, I decided to take up for the third time heredity work with a parthenogenetically reproducing insect. This time my efforts have been rewarded with some measure of success. Most of the results obtained up to the present are here submitted.

#### LIFE HISTORY AND HABITS OF *APHIS AVENÆ* FAB.

Before submitting the results of these experiments, and entering upon a discussion of them, I shall review briefly the life history and habits of the species under consideration.

As is true of aphids in general, this species propagates itself chiefly by means of parthenogenesis, but under certain conditions (probably due chiefly to climatic changes) the true sexes appear, mating occurs, eggs are deposited, and the parents die. In the case of this species, according to Pergande, the true sexes do not appear annually under out-of-doors conditions; but the asexual females live over the first winter, the true sexes being produced the next fall. Thus two years are required to complete the cycle from egg stage to egg stage.

*Aphis avenæ* lives on a large number of plants, but is especially injurious to small grains and grasses. It will frequently winter over on apple, pear, plum, or other deciduous trees. The eggs that have passed the winter out of doors usually hatch about the middle of March in most of the eastern states. It takes these young aphids about a month to reach maturity; when they are called the stem-mothers. The offspring of these stem-mothers are all asexual females, and produce parthenogenetically, for several or many generations, other asexual individuals. These asexual females are of two classes; winged and wingless. Although the winged or wingless condition of these two classes constitute the chief ground for their differentiation there are other differences also, but generally these are not very important.

During the warmer part of the season the asexual females reproduce very rapidly, and the time required for the complete life cycle may not be more than six days. During the colder parts of the year two weeks or even more may be required for the completion of the life cycle. The asexual individuals vary

greatly in their period of longevity and in their fecundity. Some will die in a few days after reaching maturity, and will leave few or no offspring. Others may live for two weeks or more, and leave at least a score of offspring.

The young when born are quite similar to the adults except in size. They at once begin to feed, and after molting three or four times they reach maturity. Although the immature individuals are quite content to settle on the same stalk next to their mother, and to remain there throughout their period of growth, when they reach maturity, especially if they are winged, they are restless, and generally leave the plant upon which they have been reared.

#### VARIATIONS.

This aphid is quite variable in several respects. Pergande, who has made a special study of the species, states: "I have found a certain range of variation in the comparative length in the joints of the antennæ, as well as in the nectaries of the progeny of the apple louse [*Aphis avenæ*], the extreme forms of which may easily induce superficial students to consider them as distinct. Large series, however, of the various forms, more or less due to the season or abundance of food, have convinced me that all of them belong to but one species."

I cannot agree with Pergande in attributing these variations entirely to the season or the food supply. For ten generations I have reared these aphids exclusively on young wheat shoots, and I find that most of these variations obtain even in their extremes when all individuals are reared on the same diet. However, the food supply certainly does affect some of the variations, but most of them originate without a change in the amount or nature of food taken. What is more significant, I find these variations existing among offspring of a single female reared under identical conditions and even find the antenna on one side differing from the antenna on the other side in the same individual. In regard to this latter point, however, I find that for a large majority of the individuals examined the antennæ on the two sides of the same individual are the same or nearly so.

After studying the different characters which were available I finally decided to use those of the antennæ. The variations in the relative lengths of the third and fourth segments were observed and employed. It is interesting to note that these characters are the same as those I selected two years ago when working with *Aphis brassicæ* Linn.; they are also the same as those used by Kelly in his work with *Aphis rumicis*.

#### METHODS.

In order to obtain as nearly as possible uniform conditions for these experiments, I reared all of the aphids on young wheat plants. These wheat shoots were never allowed to get to be more than ten or fifteen days old, and I kept them nipped back to a height of not more than three or four inches. New plants were reared from seed for each generation of plant lice. All of the plants were kept upon a single large table in the middle of the laboratory, so that changes in heat or moisture would affect all individuals of each fraternity in much the same way.

The wheat plants used were grown in small flower pots, a single plant being raised in each pot. Soon after the aphids were born they were separated, and each nymph was placed on a single wheat plant growing in its own pot. This aphid was confined by placing a small lamp chimney, covered at the top with surgeon's gauze, over the wheat plant. This would permit ready observation of the developing aphid, and would also permit the transpiration of the wheat plant. Each individual was given a label which showed the generation to which it belonged, and also its individual number in this generation. Thus, F<sub>7</sub>I<sub>4</sub> would mean individual number fourteen of the seventh filial generation.

When it came to taking measurements of the third and fourth segments of the antennæ in order to record the same and to select individuals for carrying on the strain I encountered several difficulties. At first I tried to measure these in the live adults by weighing down the insect with a cover-glass, but this would not enable me to make accurate measurements. After trying several other methods I finally decided to let each adult remain on its own wheat plant, and produce her progeny; after which

she was killed, and the head, with the antennæ, was severed from the body, cleared in Gage's mixture, and mounted in balsam on a microscope slide. This method I found to be the only satisfactory one, for two reasons. First, measurements of the segments of the antennæ could be made accurately; and second, the fecundity of the individuals could be tested before the selection was made, a very important factor, since it frequently happens that some adults have very few or no offspring.

Having made the measurements of the antennal segments, and obtained the index for the same, I selected from each fraternity the individual or individuals desired. These were usually those whose antennal index was either the lowest or the highest in the fraternity, provided they had left a sufficient number of offspring. Now the offspring of the individuals selected were separated and placed on individual plants; those of the other individuals of the fraternity were discarded.

In making the measurements of the segments of the antennæ a mechanical eye micrometer was used. Both antennæ were measured, and an average obtained from the two measurements in order to get the index for the individual. From these indices ratios were obtained, segment four being taken as unity.

Having obtained the ratio of the length of segment three in each case to the length of segment four, I have plotted (Fig. 1) the results of the selections for ten generations. For the first six generations, random selections were made in order to be sure of a pure strain and to determine the average mean index for this strain. The mean thus obtained gave a ratio of 1.80:1, that is, segment three of the antennæ was found to be one and eight tenths times as long as segment four. This ratio established for the pure line is represented by the heavy horizontal line running through about the middle of the plot in Fig. 1.

## RESULTS.

On April 9 the first individual was isolated, a wingless asexual female, and she became the mother from which all the succeeding individuals were descended. This stem mother gave birth to twenty-nine offspring. She was now killed and her antennal index taken. It was found to be 1.77:1. From the twenty-

nine offspring I selected one at random, with which to carry on the strain. The individual selected was  $F_{13}$  (that is, individual number three of the first filial generation). This individual gave birth to ten young. Her antennal index proved to be  $1.77:1$ , the same as that of her mother. From the  $F_2$  individuals I selected at random again an individual which became the mother of six offspring. Her index was, as later obtained,  $1.67:1$ , while that for the mean of her offspring was  $1.77:1$ .

For the next three generations selections were made at random, a prolific or healthy looking individual being taken. The measurements of the antennal segments of all the individuals were taken, and from these the fraternal means for the second, third, fourth, and fifth generations obtained. For the first filial generation I obtained the index of the single individual used to carry on the strain. Using this index and that of the stem mother I obtained a curve for the first five generations. This I have plotted (see Fig. 1). It will be noted here that in the case of the selections of individuals representing extreme variations, as was done in the second and third filial generations, that the mean of their offspring came back to or almost to that of the strain.

In the fourth generation an individual was selected which had an antennal formula near that for the mean of its fraternity, and exactly the same as that obtained for the strain; yet its offspring gave a mean much higher than that of any individual belonging to the fraternity from which the mother was taken! (See Fig. 1.) More than this, the mean of this fraternity was higher than the index for any individual of any fraternity previously obtained. From the individuals of the  $F_5$  generation one was obtained with a low index. It gave a brood of normal individuals.

It was from among the individuals of the  $F_6$  generation that I began making my selections in an attempt to obtain two strains, one with a high antennal formula, the other with a low antennal formula, from this isolated pure line of parthenogenetically reproducing plant lice.  $F_{65}$ , with a formula of  $1.88:1$ , was selected for obtaining a strain with a high index;  $F_{63}$ , formula  $1.66:1$ , was taken for obtaining a strain with a low index.  $F_{65}$

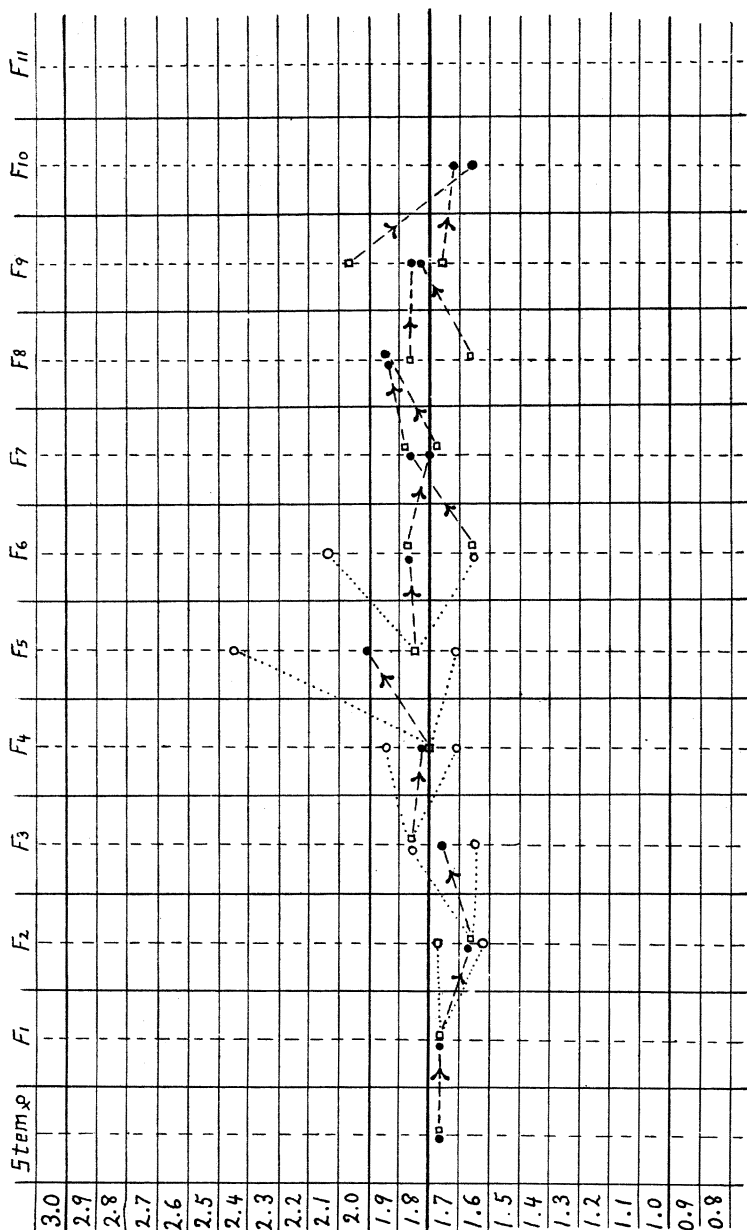


FIG. 1. Diagram showing the plotted results of selections within a pure line of *Aphis arenae* Fab. Each black circular spot represents the position of a fraternal mean; the open circles represent the positions of the extreme variants of a fraternity; each square represents the position of the individual selected for carrying on the strain or pseudostrains. The arrows indicate the course taken by the strain as it passes from the selected individual to the mean of its offspring (the fraternity of the next generation). The heavy line at 1.8 represents the position of the mean of the strain, and may be called the mean-of-the-strain base line.



TABLE OF MEASUREMENTS AND RATIOS.

Generation and No. of Individual.	Wings.	Left Antenna.		Right Antenna.		Average for Both Antennæ.		Ratio.
		3d Jt.	4th Jt.	3d Jt.	4th Jt.	3d Jt.	4th Jt.	
Stem ♀ . . . .	—	3.20	1.80	Lost	.....	3.20	1.80	1.77:1
F <sub>13</sub> . . . . .	—	3.70	1.80	3.70	2.25	3.70	2.025	1.82:1
F <sub>21</sub> . . . . .	—	3.40	1.95	3.20	2.00	3.30	1.975	1.67:1
F <sub>23</sub> . . . . .	—	3.35	1.80	3.15	1.90	3.25	1.85	1.78:1
F <sub>28</sub> . . . . .	—	3.50	2.15	Lost	.....	3.50	2.15	1.63:1
F <sub>31</sub> . . . . .	—	2.95	1.50	2.90	1.65	2.925	1.575	1.86:1
F <sub>33</sub> . . . . .	—	2.70	1.65	2.50	1.50	2.60	1.575	1.65:1
F <sub>35</sub> . . . . .	—	3.05	1.60	2.85	1.70	2.95	1.65	1.79:1
F <sub>41</sub> . . . . .	—	2.40	1.40	Broken off		2.40	1.40	1.71:1
F <sub>43</sub> . . . . .	—	2.35	1.25	2.15	1.25	2.25	1.25	1.80:1
F <sub>46</sub> . . . . .	—	Broken off		2.45	1.25	2.45	1.25	1.96:1
F <sub>51</sub> . . . . .	—	2.70	1.10	2.70	1.10	2.70	1.10	2.45:1
F <sub>52</sub> . . . . .	—	2.65	1.10	2.15	1.00	2.40	1.05	2.28:1
F <sub>53</sub> . . . . .	—	3.15	1.75	3.20	1.85	3.175	1.80	1.76:1
F <sub>56</sub> . . . . .	—	2.80	1.50	2.80	1.75	2.80	1.625	1.72:1
F <sub>55</sub> . . . . .	—	3.75	1.80	3.30	1.65	3.525	1.725	2.04:1
F <sub>510</sub> . . . . .	—	3.70	1.80	3.70	2.20	3.70	2.00	1.85:1
F <sub>61</sub> . . . . .	—	2.75	1.50	2.75	1.50	2.75	1.50	1.83:1
F <sub>63</sub> . . . . .	—	3.10	1.85	3.15	1.90	3.125	1.875	1.66:1
F <sub>65</sub> . . . . .	—	3.05	1.65	3.25	1.70	3.15	1.675	1.88:1
F <sub>66</sub> . . . . .	—	3.15	1.70	Broken off		3.15	1.70	1.85:1
F <sub>62</sub> . . . . .	+	Broken off		3.60	1.80	3.60	1.80	2.00:1
F <sub>64</sub> . . . . .	+	3.25	1.65	3.70	1.60	3.475	1.625	2.14:1
F <sub>73</sub> . . . . .	—	3.60	2.00	3.65	1.82	3.625	1.91	1.89:1
F <sub>74</sub> . . . . .	—	3.30	1.85	3.40	1.90	3.35	1.875	1.79:1
F <sub>72</sub> . . . . .	—	4.00	2.00	3.80	2.20	3.90	2.10	1.86:1
F <sub>76</sub> . . . . .	—	Lost	.....	4.15	2.10	4.15	2.10	1.98:1
F <sub>78</sub> . . . . .	—	3.85	2.25	Lost	.....	3.85	2.25	1.71:1
F <sub>711</sub> . . . . .	—	3.70	1.95	Broken off		3.70	1.95	1.90:1
F <sub>81</sub> . . . . .	—	4.60	2.55	4.60	2.40	4.60	2.475	1.86:1
F <sub>812</sub> . . . . .	—	3.55	1.75	3.50	2.10	3.525	1.925	1.83:1
F <sub>82</sub> . . . . .	+	4.70	2.25	4.70	2.40	4.70	2.325	2.02:1
F <sub>83</sub> . . . . .	+	Misplaced		4.95	2.50	4.95	2.50	1.98:1
F <sub>84</sub> . . . . .	+	4.30	2.20	4.70	2.45	4.50	2.325	1.93:1
F <sub>85</sub> . . . . .	+	3.70	1.95	3.95	2.00	3.825	1.975	1.99:1
F <sub>86</sub> . . . . .	+	4.20	2.05	3.75	2.00	3.975	2.02	1.91:1
F <sub>87</sub> . . . . .	+	4.10	2.20	4.00	2.05	4.05	2.125	1.90:1
F <sub>88</sub> . . . . .	+	4.00	2.00	Broken off		4.00	2.00	2.00:1
F <sub>810</sub> . . . . .	+	Broken off		4.75	2.40	4.75	2.40	1.98:1
F <sub>811</sub> . . . . .	+	4.20	2.16	3.85	2.20	4.025	2.18	1.85:1
F <sub>813</sub> . . . . .	—	4.20	2.30	4.15	2.30	4.175	2.30	1.81:1
F <sub>816</sub> . . . . .	—	3.40	1.17	3.40	1.17	3.40	1.17	2.90:1
F <sub>817</sub> . . . . .	—	3.80	2.25	3.75	2.15	3.775	2.20	1.71:1
F <sub>819</sub> . . . . .	—	3.60	2.20	3.60	2.10	3.60	2.15	1.67:1
F <sub>814</sub> . . . . .	+	4.10	2.30	4.10	2.30	4.10	2.30	1.78:1
F <sub>815</sub> . . . . .	+	4.25	2.15	Broken off		4.25	2.15	1.97:1
F <sub>818</sub> . . . . .	+	3.40	1.80	3.20	1.80	3.30	1.80	1.83:1
F <sub>817</sub> . . . . .	+	3.20	1.80	Displaced		3.20	1.80	1.77:1
F <sub>818</sub> . . . . .	+	3.35	1.80	3.05	1.80	3.20	1.80	1.77:1
F <sub>819</sub> . . . . .	+	4.00	2.20	Broken off		4.00	2.20	1.81:1
F <sub>920</sub> . . . . .	+	3.85	1.75	3.75	1.95	3.80	1.85	2.05:1
F <sub>922</sub> . . . . .	+	3.60	2.05	3.60	2.00	3.60	2.025	1.77:1
F <sub>91</sub> . . . . .	+	3.30	2.00	3.35	2.00	3.235	2.00	1.66:1
F <sub>92</sub> . . . . .	+	Broken off		3.35	1.75	3.35	1.75	1.91:1

TABLE OF MEASUREMENTS AND RATIOS (*Continued*).

Generation and No. of Individual.	Wings.	Left Antenna.		Right Antenna.		Average for Both Antennæ.		Ratio.
		3d Jt.	4th Jt.	3d Jt.	4th Jt.	3d Jt.	4th Jt.	
F <sub>93</sub> .....	+	Broken off		Broken off		.....	.....	.....
F <sub>94</sub> .....	+	Broken off		3.40	2.00	3.40	2.00	1.70:1
F <sub>95</sub> .....	+	3.20	1.75	3.35	1.95	3.275	1.85	1.77:1
F <sub>96</sub> .....	+	3.80	1.80	3.30	1.70	3.55	1.75	2.03:1
F <sub>98</sub> .....	+	3.60	1.85	3.35	2.00	3.475	1.925	1.80:1
F <sub>99</sub> .....	-	3.70	1.80	3.80	1.80	3.75	1.80	2.08:1
F <sub>101</sub> .....	+	2.90	1.80	3.10	1.75	3.00	1.775	1.70:1
F <sub>102</sub> .....	+	Broken off		2.80	1.75	2.80	1.75	1.60:1
F <sub>103</sub> .....	+	3.00	1.65	Displaced		3.00	1.65	1.82:1
F <sub>104</sub> .....	-	3.15	1.80	3.00	1.85	3.075	1.825	1.63:1
F <sub>105</sub> .....	-	2.50	1.50	2.50	1.50	2.50	1.50	1.66:1
F <sub>106</sub> .....	-	3.25	1.90	3.30	2.05	3.275	1.975	1.65:1
F <sub>107</sub> .....	-	2.50	1.60	2.50	1.60	2.50	1.60	1.56:1
F <sub>1011</sub> .....	-	2.40	1.40	Broken off		2.40	1.40	1.71:1

gave me five young, only two of which came to maturity and gave an average index of 1.80:1. F<sub>63</sub> gave birth to eight individuals, four of which came to maturity, and gave as a fraternal mean an index of 1.88:1. Although the number of individuals obtained are too small to draw any conclusions, if they were not supported by a repetition of similar results, yet they are very significant, as is shown by the plot in Fig. 1. The curves running from the two extreme individuals selected of the F<sub>6</sub> generation, to the fraternal means of the offspring of these two individuals actually cross! In other words, offspring from an individual with a high index had a lower fraternal mean than the offspring from the individual (of the same fraternity as the former) with a low index. Among the F<sub>7</sub> individuals two were selected; one, F<sub>73</sub> with an index of 1.89:1, and one, F<sub>74</sub>, with an index of 1.79:1. From the former, F<sub>73</sub>, eleven young were reared to maturity. They gave a fraternal mean of 1.93:1. This is almost the same formula as was obtained for the mean of the offspring of the latter individual, F<sub>74</sub>, which was 1.95:1. Here we get convergence almost to the same point in the offspring of two variants of a fraternity. However, both of these fraternities, that is, of the F<sub>8</sub> generation, did not show a reversion toward the mean of the original strain, but a deviation from it. This is what occurred in the case of the F<sub>5</sub> generation. In the F<sub>8</sub> fraternity, F<sub>81</sub>, formula 1.86:1, and F<sub>819</sub>, formula 1.67, were

selected, each being a descendent of a different individual of  $F_7$  generation.  $F_{81}$  gave offspring with a mean of  $1.85:1$ , and  $F_{819}$  offspring with a mean of  $1.83:1$ . The former converged slightly toward the mean base line of the original strain, the latter reverted not only to it but beyond it, so that the means of the two fraternities almost meet. From these fraternities  $F_{99}$ , formula  $2.08:1$ , and  $F_{917}$ , formula  $1.77:1$ , were taken, each again being selected from the different pseudostrain. Although the former had an antennal formula very high,  $2.08:1$ , in fact higher than that of any individual selected during the whole experiment, yet its seven offspring gave the remarkably low fraternal mean of  $1.66:1$ . Thus reversion in this case was not to the mean of the original strain but much beyond it, as has been noted before in the case of selections from the  $F_6$  and  $F_8$  generations. From  $F_{917}$ , only a single individual was obtained which gave a formula of  $1.71:1$ , a slight deviation from the mean base line.

#### CONCLUSIONS.

The following conclusions can be drawn from the results obtained. Selections from among extreme variants do not alter the mean as obtained for the strain without selection. The fraternal mean of any generation may show a great fluctuation from the mean of the strain, but this fluctuation is not transmitted to following generations. The offspring of an extreme variant may show not a reversion to the mean of the line or strain, but a reversion which swings pendulum-like much beyond this mean, only to be brought back to its former side of the mean-of-the-strain base line in the next generation. This phenomenon I call oscillating reversion. Great deviations from the mean of the strain occur among fraternities which have been produced by individuals whose formula is almost the same as that of the mean of the strain. This great divergence is due to some underlying cause not yet determined, and is independent of the nature or amount of food.

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